

Life History Patterns of *Discorsopagurus schmitti*, a Hermit Crab Inhabiting Polychaete Tubes

FRANCESCA GHERARDI¹ AND PAUL M. CASSIDY²

¹*Dipartimento di Biologia Animale e Genetica "Leo Pardi," Università di Firenze, Via Romana 17, 50125 Firenze, Italy; and* ²*Shannon Point Marine Center, Western Washington University, 1900 Shannon Point Rd., Anacortes, Washington 98221*

Abstract. *Discorsopagurus schmitti* is a hermit crab that inhabits empty polychaete tubes in the North Pacific. Here we describe some aspects of its life history (relative growth, population structure, reproductive biology, and incidence of parasitism) and discuss the relationships among them. Unlike most hermits, the two sexes of this species have similar size distributions. In both sexes, larger body size is accompanied by a higher reproductive output (larger clutch size in females and more intrasex competitive potential in males). The energy the females expend in egg production might be equaled in this species by the energy the males expend in supporting parasites. In fact, the extent of infestation by two rhizocephalans [*Peltogaster boschmae* and *Thilacoplethus* (= *Thompsonia reinhardi*)] is more pronounced in males, especially those in the larger size classes. However, rhizocephalans have little effect on their hosts; growth and secondary sexual characters are not influenced. The only morphological modification is the more frequent loss of the second pleopod. Infected hermits also showed a mock parental behavior, fanning the externae with the pleopods as ovigerous females fan their eggs. Larvae are released in sequential bursts, and hatching occurs exclusively at night, possibly to minimize predation by diurnal fishes. Hatching is also synchronized with neap tides, which might keep the larvae from being flushed out into open waters. In a species whose habitat (sabellarian bioherms) is rare and quite unpredictable, it is beneficial to retain larvae near the parental population.

Introduction

Discorsopagurus schmitti (Stevens, 1925) is an anomuran crab that occurs widely along the North Pacific

coasts from Japan to Puget Sound (McLaughlin, 1974). In both its geographical distribution and its ecological role, this species is strictly dependent on the polychaete *Sabellaria cementarium* Moore, 1906. The hermit uses attached worm tubes as housing and occupies a niche within the community associated with sabellarian bioherms (Gherardi and Cassidy, 1994a). A bioherm is a rock formed by accretions from sedentary organisms and surrounded by other kinds of rocks. Within the habitat, *D. schmitti* has a contagious distribution, the crabs occurring with a density averaging 6 specimens per dm² (Gherardi and Cassidy, 1994b).

Despite its peculiar habits and widespread distribution, the main life history traits of the species are still unknown. Previous papers were concerned only with its adaptations to the sessile worm tubes (Caine, 1980) and its ecology (Gherardi and Cassidy, 1994b). Our study investigates the relative growth, population structure, reproductive biology, and incidence of parasitism by rhizocephalans in *D. schmitti*.

Materials and Methods

D. schmitti was collected from a wide sabellarian bioherm in Burrows Channel, Fidalgo Island (northern Puget Sound, Washington). A total of 440 specimens were collected: 329 from June to August 1992, and 111 from January to April 1993. See Gherardi and Cassidy (1994a, b) for details on habitat and sampling procedure.

Sixty-four animals were individually weighed to the nearest 0.01 g. Chelipeds were excluded from the weight because they are variable and sometimes absent. For each specimen, we recorded sex, size (shield length, SL, to the nearest 0.1 mm), missing chelipeds (*i.e.*, the number of "injured" specimens), and the number and maximum

diameter of any egg present. When possible, the maximum axis of the occupied polychaete tube was measured with a caliper. The number and position of externae of the parasitic rhizocephalans *Peltogaster boschmae* Reinhard and *Thilacoplethus* (= *Thompsonia*) *reinhardi* Lützen were also noted. Because we did not assess the presence of rootlets penetrating major organs (stage of interna), which precedes the parasite's sexual development, we may have underestimated the extent of infestation within the sample.

To describe the format of relative growth (*i.e.*, the change in shape with growth; Hartnoll, 1982), we measured the length of the dactyl (DL) and palm (PA) of both chelae, and their depth (DE) in 130 hermits. To represent the patterns of the relative growth of these measures (y) with respect to the SL as an independent variable (x), the natural logarithmic transformation ($\ln y = \ln a + b \ln x$) of the exponential function $y = a x^b$ was used. This relationship fits nearly all the instances of allometric growth in crustaceans (Hartnoll, 1982). The values of b define the type of allometry ($b = 1$: isometry; $b < 1$: negative allometry; $b > 1$: positive allometry). This and the other parameters of $\ln y$ on $\ln x$, calculated using the Least-Squares Method, allowed us to use standard tests for significance and to compare slopes and intercepts between groups.

Within winter samples, pleopods were examined and their configuration related to the occurrence of parasites. The configuration of pleopods in *D. schmitti* was first described by McLaughlin (1974); the species shows pleopods 2–5, with the exception of some males, in which the second pleopod is absent.

The behavior of animals occupying pieces of transparent glass tubing was recorded with a Panasonic color camera and played back on a Mitsubishi recorder.

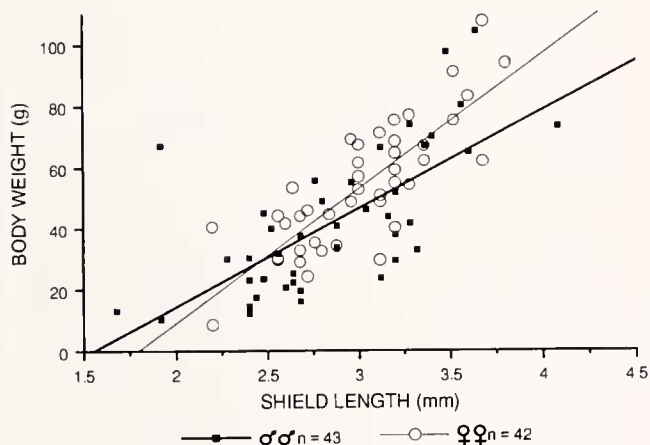


Figure 1. Relationship between size (shield length) and body (without chelipeds) weight, compared between sexes. A positive correlation was found in both males ($r = 0.692$, $df = 41$, $P < 0.01$), and females ($r = 0.809$, $df = 40$, $P < 0.01$).

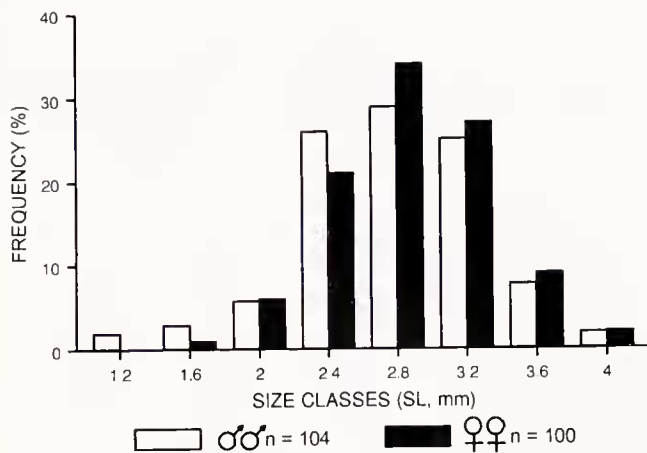


Figure 2. Size class distributions compared between sexes from summer collections.

Data on egg incubation and hatching were obtained from 19 ovigerous females, collected on January 18 (5), February 8 (5), and April 27 (9) 1993. In the laboratory, the females were placed in individual glass bowls 20 cm in diameter, in filtered seawater with a salinity of 28–31‰. The bowls were kept in a constant temperature unit at 10°C under a light:dark regime of 14:10. Until they released larvae, ovigerous females were checked twice a day for hatching, placed in bowls of clean seawater, and fed *Artemia*. The number of larvae released daily was recorded for ten of the females.

For statistical analysis, we followed the methods and recommendations of Siegel (1956) and Zar (1984). The level of significance under which the null hypothesis was rejected is $\alpha = 0.05$.

Results

Population structure

Figure 1 shows the relationship between SL and body weight (excluding chelipeds) compared between sexes. No between-sex difference was found in either the slope (32.12 vs. 43.96, $t = 1.549$, $df = 81$, ns) or the intercept (−49.90 vs. −78.98, $t = 1.781$, $df = 82$, ns) of the regression line.

The sizes of crabs (SL) during summer were analyzed (Fig. 2). No significant difference in size distributions was found between the two sexes ($G = 4.442$, $df = 7$, ns). The smallest specimens measured 1.1 (prepubertal, showing no gonopores), 1.4 (male), and 1.9 mm SL (female), and the maximum size attained 3.9 mm SL in the two sexes.

The sex ratio was 50.98% (104 males to 100 females), which did not differ from 1:1 ($\chi^2 = 0.044$, $df = 1$, ns). Similarly, the sexes remained balanced when three size classes were distinguished (<2.6 mm SL: $\chi^2 = 0.5$, $df = 1$, ns; 2.6–3.4 mm SL: $\chi^2 = 0$, $df = 1$, ns; >3.4 mm SL: $\chi^2 = 0$, $df = 1$, ns).

Table I

Isometric or allometric growth with size of *Discorsopagurus schmitti* (shield length) of three measures of both the major (right) and the minor (left) chela, compared between sexes

ln shield length vs.:	♂♂				♀♀			
	<i>r</i>	<i>b</i>	<i>t</i> <i>b</i> ≠ 1	<i>a</i>	<i>r</i>	<i>b</i>	<i>t</i> <i>b</i> ≠ 1	<i>a</i>
ln DC (major chela)	0.721	0.79	2.173	0.13	0.337	0.40	4.367*	0.65
ln PA (major chela)	0.878	0.66	7.450*	0.12	0.624	0.47	7.435*	0.36
ln DE (major chela)	0.900	0.84	3.010*	-0.04	0.740	0.57	6.727*	0.33
ln DC (minor chela)	0.831	0.70	4.928*	-0.07	0.484	0.41	6.590*	0.31
ln PA (minor chela)	0.811	0.60	7.238*	-0.04	0.682	0.51	7.371*	0.07
ln DE (minor chela)	0.634	0.48	6.831*	0.19	0.752	0.56	7.445*	0.11

DC = dactyl length; PA = palm length; DE = chela depth.

a = intercept of the regression line.

* $P < 0.01$.

All the correlation coefficients (*r*) are significant ($P < 0.01$). Isometry is satisfied when the regression coefficient (*b*) equals 1 after Student's *t*-test (*t*), otherwise an allometric growth (here only negative) occurs. The numbers of males and females are 63 and 69, respectively.

The size and sex of specimens in three individually collected clumps were separately analyzed; the comparison did not show any difference in either size distribution ($G = 6.08$, $df = 4$, ns) or sex ratio ($\chi^2 = 1.458$, $df = 2$, ns).

Chelipeds

The growth of both chelae relative to hermit size (SL) was always negatively allometric for DC, PA, and DE, with the exception of the DC of the major chela in the males, where it was isometric (Table I). Table II gives the between-sex differences in the parameters of the regression lines; the males had a more voluminous major chela than similarly sized females, as well as a longer dactyl in the minor chela. However, the male and female regression

lines crossed at a large crab size (major chela: 3.8, 3.4, 4.1 mm SL for DC, PA, and DE, respectively; minor chela DC: 3.7 mm SL).

In all the examined specimens, the right chela was the major one. This had constantly higher values than the left one with SL increment (equal slope, but a higher intercept), with the exception of the major chela DE, where the growth increased with size (Table III).

Injured specimens represented 24.11% of the sample, without any significant difference between sexes (25% in males, 24.26% in females: $\chi^2 = 1.762$, $df = 1$, ns). Right

Table II

Between-sex comparison of chelar growth in *Discorsopagurus schmitti*

	<i>t</i>	<i>b</i>	♂ vs. ♀	<i>t</i>	<i>a</i>	♂ vs. ♀
DC (major chela)	2.298*		>	—		—
PA (major chela)	2.265*		>	—		—
DE (major chela)	3.190**		>	—		—
DC (minor chela)	2.734**		>	—		—
PA (minor chela)	1.003		=	0.301		=
DE (minor chela)	0.713		=	1.428		=

— test not applicable.

DC = dactyl length; PA = palm length; DE = chela depth.

* $P < 0.05$; ** $P < 0.01$.

Comparisons after Student's *t*-test (*t*) between sexes in both the slope (*b*) and the intercept (*a*) of the regression lines (after a ln-ln transformation) describing the relationships between hermit size (shield length) and three chelar measures. The degrees of freedom are 127 and 128.

Table III

Between-side comparison of chelar growth in *Discorsopagurus schmitti*

♂♂:	<i>b</i>		<i>a</i>	
	<i>t</i>	<i>r</i> vs. <i>l</i>	<i>t</i>	<i>r</i> vs. <i>l</i>
DC	0.755	=	16.342**	>
PA	0.847	=	20.505**	>
DE	3.935**	>	—	—
♀♀:	<i>b</i>		<i>a</i>	
	<i>t</i>	<i>r</i> vs. <i>l</i>	<i>t</i>	<i>r</i> vs. <i>l</i>
DC	0.037	=	17.964**	>
PA	0.418	=	21.289**	>
DE	1.636	=	24.428**	>

— test not applicable.

DC = dactyl length; PA = palm length; DE = chela depth.

** $P < 0.01$.

Comparison after Student's *t*-test (*t*) between the right (*r*) and the left (*l*) chela in both the slope (*b*) and the intercept (*a*) of the regression lines (after a ln-ln transformation) describing the relationships between hermit size (shield length) and three chelar measures. The degrees of freedom are 121, 122 in males, and 134, 135 in females.

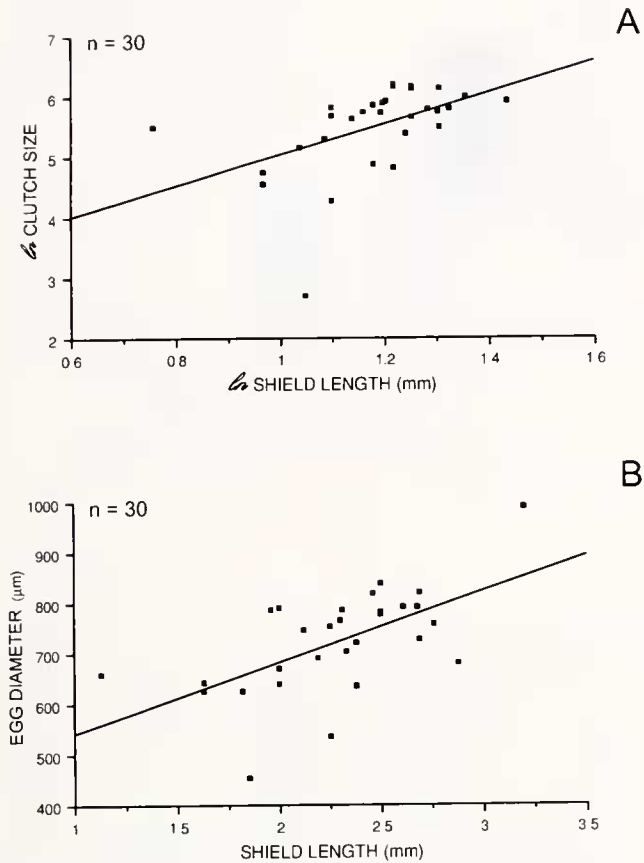


Figure 3. Relationships between the size of ovigerous females (shield length) and both the number (after a ln-ln transformation, A) and the diameter (maximum axis, B) of the spawned eggs.

chelipeds were missing more often than left ones (65.96% vs. 34.04%, $\chi^2 = 4.17$, $df = 1$, $P < 0.05$).

Eggs

Egg-bearing females occurred in winter samples only. They were first found in January and were still present at the end of April, though their percentage was low (20%, 9 out of 45). Their numbers did not differ from those of nonovigerous females (January 18: 19 vs. 10, $\chi^2 = 2.207$, $df = 1$, ns; February 1: 15 vs. 21, $\chi^2 = 0.694$, $df = 1$, ns), and specimens in the two reproductive states shared the same size distribution ($G = 2.906$, $df = 5$, ns) and frequency per size class (<2.6 mm SL 45.10%, vs. a uniform distribution: $G = 0.486$, $df = 1$, ns; ≥ 2.6 mm SL 70%, $G = 1.567$, $df = 1$, ns). The smallest and largest females found bearing eggs measured, respectively, 1.1 and 3.2 mm SL.

Egg number per clutch ranged from 14 to 496, averaging 287. Female size (SL) was positively correlated with the number of eggs (after a ln-ln transformation: $r = 0.478$, $df = 28$, $P < 0.01$, $b = 2.56$, $a = 2.48$) (Fig. 3A). The

value of the correlation coefficient did not significantly differ from 3 ($t = 0.495$, $df = 28$, ns); that is, clutch size is proportional to the cube of the SL (roughly equaling the body mass).

The mean egg diameter was 722 μm (SE = 19, $n = 30$), ranging from 455 to 990 μm . A positive correlation was also found between the SL of the female and the average diameter of her eggs ($r = 0.586$, $df = 28$, $P < 0.01$, $b = 0.14$, $a = 0.40$) (Fig. 3B), showing that bigger females produce larger (and more numerous) eggs.

Eggs are attached to the second through the fourth pleopods, about 100 per pleopod, in bunches of 7 to 15. They are slightly ovate and attached by a funiculus, measuring around 1.2 mm. Ovigerous females kept inside transparent tubing were seen fanning the eggs with a reversing current created by the second and third pleopods.

Hatching

Hatching occurred between 1 and 75 days ($n = 17$) after collection. Because all the analyzed females bore eggs when collected, this is only a minimum estimate of the actual length of egg incubation.

The number of larvae per individual ranged from 80 to 541 (average = 226, SE = 46) in the 10 females analyzed, and did not differ significantly from the number of eggs per batch ($t = 1.31$, $df = 38$, ns), being on average 98.74% of the eggs spawned. Larvae were released in 3–6 days (average = 5.1 day, SE = 0.3), with a maximum of 209 larvae in the fourth day. No correlation was found between the length of the hatching period and the female size ($r = 0.074$, $df = 8$, ns), but the former was positively related to the overall number of larvae (Spearman rank correlation test: $r_s = 0.742$, $t = 3.134$, $df = 8$, $P < 0.02$). Larvae were not released at a constant rate; the percentage released (Fig. 4) differed significantly throughout the hatching period (Kruskal-Wallis one-way analysis of vari-

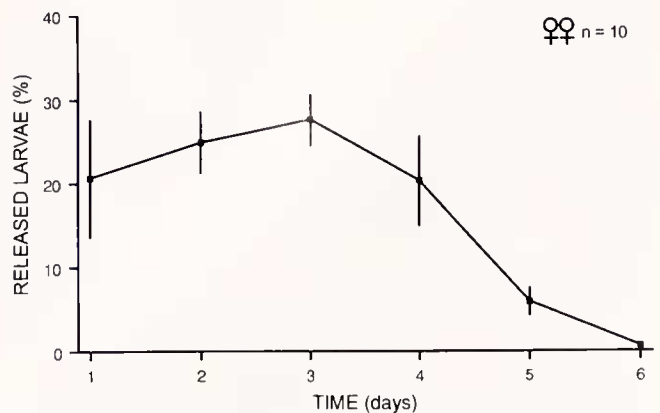


Figure 4. Percentage (average \pm SE) of the larvae released by 10 females plotted against the length of hatching (in days).

ance: $H = 29.975$, $df = 5$, $P < 0.001$), peaking in the third day and then falling off abruptly after the fifth day.

Hatching occurred exclusively at night, and mostly during the neap phase of the tide (Mann-Whitney test: $U = 0$, $n = 7$ and 7 , $P < 0.01$), when the mean tidal current is consistently slower (Fig. 5). For our comparison, we defined neap (or spring) phase as the day of the minimum (or maximum) tidal excursion for a lunar tidal cycle plus the 3 days preceding and following that date.

Parasite distribution

Peltogaster boschmae was the most common rhizocephalan parasite in our samples, affecting 18.5% of the specimens; *Thilacoplethus* (= *Thompsonia*) *reinhardi* infected 6.8%; and the two rhizocephalans co-occurred in 2.5%. These figures are similar to the percentages reported by Lützen (1992) for a previous study in the same area.

A sexual difference in the degree of infestation was seen in both the number of externae per individual (males: average = 2.9, SE = 0.6; females: average = 2.3, SE = 0.9; $\chi^2 = 9.312$, $df = 2$, $P < 0.01$) (Fig. 6) and the prevalence of parasitism (*i.e.*, the percentage of the parasitized hermits; Margolis *et al.*, 1982) (males vs. females: 28.17% vs. 14.39%, $\chi^2 = 7.144$, $df = 1$, $P < 0.01$). Similar results were obtained from the winter samples, where parasitized males and females scored 28.26% and 9.37% respectively ($\chi^2 = 5.424$, $df = 1$, $P < 0.02$). The number of parasitized specimens did not differ between sampling periods (summer: 60 out of 281, winter: 19 out of 110; $\chi^2 = 0.01$, $df = 1$, ns).

The maximum number of externae from the summer samples was 15 in males and 18 in females. We counted 23 externae in one female collected in winter. None of the ovigerous females in our sample had parasites (0 vs. 20% in nonovigerous ones; $\chi^2 = 5.334$, $df = 1$, $P < 0.05$). Only one female has been collected bearing both eggs and

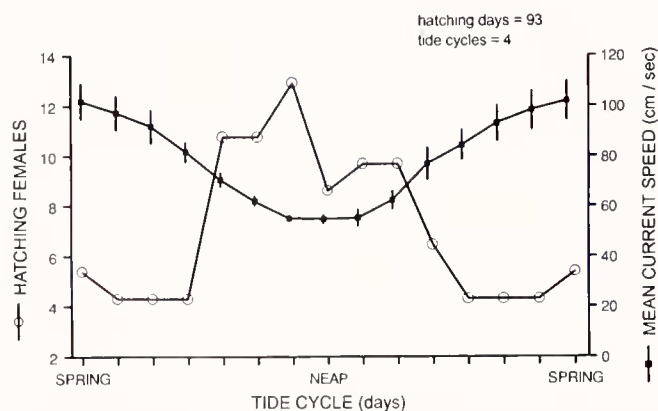


Figure 5. Occurrence of hatching within a lunar tidal cycle, compared with the mean tidal current speed per day (average \pm SE).

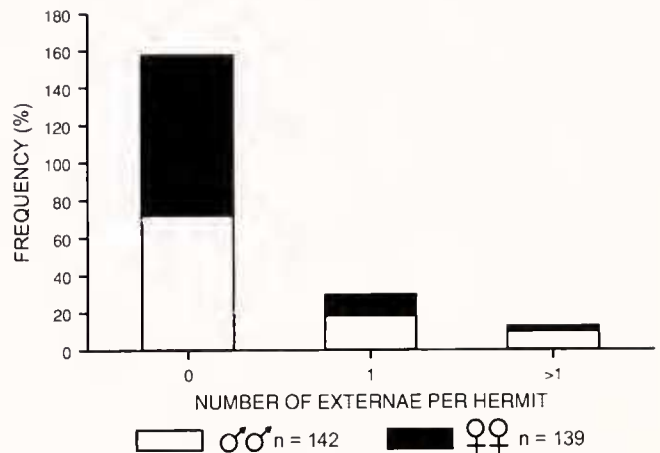


Figure 6. Number of the externae of rhizocephalan parasites per hermit host, compared between sexes.

three externae (P. M. Cassidy, pers. obs.), but it is plausible that infestation occurred after spawning. The number of externae was significantly correlated with the host size if the host was male (Spearman rank correlation test: $r_s = 0.413$, $t = 2.759$, $df = 37$, $P < 0.01$), but not if it was female ($r_s = 0.299$, $t = 1.331$, $df = 18$, ns).

The frequency distribution per size class of the infested specimens compared with respect to the healthy ones did not show any difference in the males ($G = 4.816$, $df = 3$, ns) (Fig. 7A); a difference (though slight) was found in the females, where parasites occurred more often within smaller size classes ($G = 6.913$, $df = 3$, P ca. 0.05) (Fig. 7B). When three size classes were distinguished, no between-sex difference was found in small specimens ($G = 0.004$, $df = 1$, ns), but the difference was significant in larger classes (intermediate: $G = 10.643$, $df = 1$, $P < 0.01$; biggest: $G = 2.744$, $df = 1$, P ca. 0.05). The minimum size of parasitized specimens was 1.8 in females and 1.4 mm SL in males.

Peltogaster boschmae externae never exceeded two per individual. They were more frequently found on the left side of the hermit abdomen (left, center, and right vs. a uniform distribution: $\chi^2 = 76.513$, $df = 2$, $P < 0.001$), and at the proximal end, close to the carapace (proximal, middle, distal vs. a uniform distribution: $\chi^2 = 34.241$, $df = 1$, $P < 0.001$), without any difference between sexes (side: $G = 1.118$, $df = 2$, ns; extremity: $\chi^2 = 0.029$, $df = 1$, ns). Their first point of eruption corresponded to the position of the second pleopod. In contrast, the externae of *Thilacoplethus* (= *Thompsonia*) *reinhardi*, ranging from 1 to 23, were more clumped on the host, equally distributed on the right and left halves of the hermit body, and more diffused, involving the dorsal side of the abdomen, the cephalothorax, and even the pereopods and chelipeds.

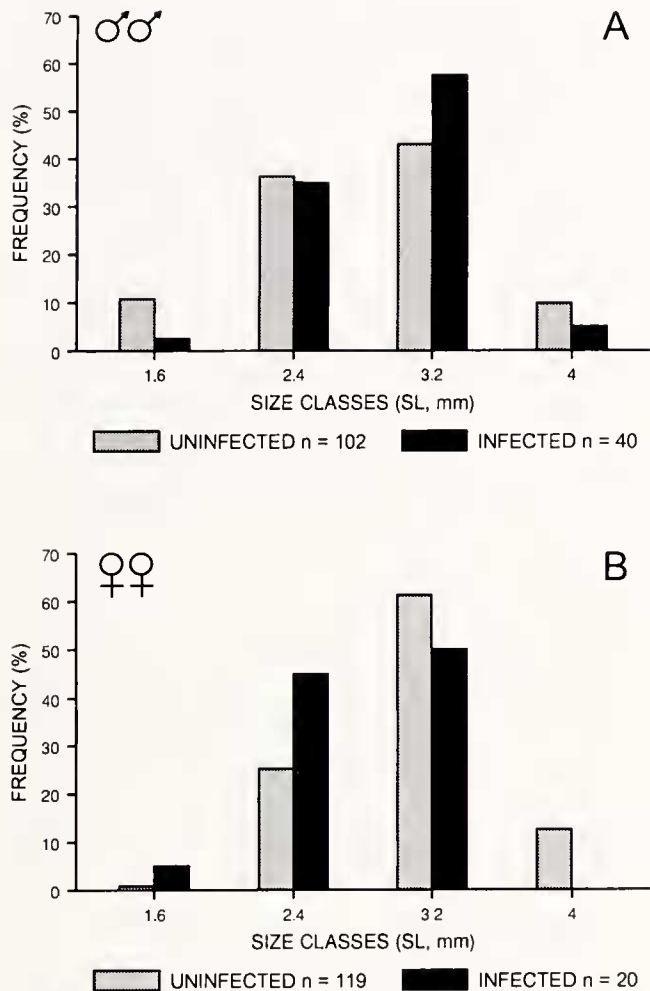


Figure 7. Size frequency distributions compared between hermits that were either uninfected or infected by rhizocephalan parasites in males (A) and females (B).

Parasites' effects on the host external morphology and behavior

To evaluate the effect of parasites on their hosts, we examined various aspects of the hermit external morphology. The pleopod number did not show any significant difference between infested and noninfested specimens in either sex (distinguishing animals with 4, 3, and less than 3 pleopods, males: $G = 1.645$, $df = 2$, ns; females: $G = 0.31$, $df = 2$, ns). However, the second pleopod was absent more often in parasitized specimens (7 out of 16 vs. 5 out of 54; $G = 8.333$, $df = 1$, $P < 0.01$). The difference was more pronounced in the males (6 out of 12 vs. 5 out of 31; $G = 4.576$, $df = 1$, $P < 0.05$) than in females (1 out of 5 vs. 0 out of 23; $G = 1.839$, $df = 1$, ns).

The relative growth of the DE of the major chela, one "maleness" character, was analyzed. No difference was found between parasitized and unparasitized specimens,

either in males (after a ln-ln transformation: b , 0.63 vs. 0.93, $t = 1.772$, $df = 56$, ns; a , 0.21 vs. -0.15 , $t = 1.847$, $df = 57$, ns) or in females (b , 0.52 vs. 0.57, $t = 0.237$, $df = 63$, ns; a , 0.40 vs. 0.33, $t = 0.011$, $df = 64$, ns). Analogously, parasites seemed not to affect hermit relative body weight in either sex (after ln-ln transformation, SL vs. weight without chelae, males: b , 3.45 vs. 5.08, $t = 1.539$, $df = 39$, ns; a , -1.13 vs. -3.31 , $t = 0.043$, $df = 40$, ns; females: b , 1.70 vs. 3.59, $t = 0.778$, $df = 38$, ns; a , 1.32 vs. -1.04 , $t = 1.216$, $df = 39$, ns). The same was also true when cheliped weight was examined (males: b , 8.80 vs. 7.26, $t = 0.537$, $df = 24$, ns; a , -15.41 vs. -11.97 , $t = 0.858$, $df = 25$, ns; females: b , -2.19 vs. 6.41, $t = 1.664$, $df = 22$, ns; a , 13.89 vs. -9.34 , $t = 1.043$, $df = 23$, ns).

Several parasitized hermits were seen molting and preserved their externae after the ecdysis, even when externae belonged to the latest stages, already containing oocytes and embryos (Lützen, 1992).

One possible behavioral effect of parasites is lethargy, which might reduce the ability of naked hermits to find empty tubes. However, in pilot experiments in the laboratory, parasitized and unparasitized *D. schmitti* individuals were about equally matched when competing for a single empty tube. In the field, no difference was seen in the relative opening diameter of the occupied tubes between hermits belonging to the two conditions (males: b , $t = 0.025$, $df = 64$, ns, a , $t = 0.169$, $df = 65$, ns; females: b , $t = 0.86$, $df = 68$, ns, a , $t = 1.913$, $df = 69$, ns).

Parasitized specimens of both sexes placed inside transparent tubing were seen fanning the externae of *Peltoaster boschmae*. The behavior was the same as that already described for ovigerous females fanning their eggs.

Discussion

The structure of the *D. schmitti* population

In the species of hermit crabs studied to date (Table IV), sex ratio in relation to size mostly follows the "anomalous" pattern described by Wenner (1972). This implies that sexes in small size classes are approximately balanced, a large excess of females is found in intermediate size classes, and an excess of males is found in the largest ones. Exceptions are reported by Wenner (1972) in *Clibanarius zebra* and *Calcinus latens*, by Abrams (1988) in *Pagurus ochotensis* and *P. aleuticus*, and by Gherardi and McLaughlin (1994) in *Calcinus laevimanus* from the Mascarenes. A further exception is *D. schmitti*, in which an equal number of males and females are represented in each size class.

One obvious bias in the size distribution analysis is the large- or small-scale habitat segregation between sexes. Species have been reported to show between-sex differences in habitat utilization (e.g., males of *Pagurus hirsutiuseculus* occupy high tidepools, but females are dom-

Table IV

Species of hermit crabs reported from the literature following the "anomalous" pattern (Wenner, 1972) in the sex-ratio-to-size relation

Genus	Species	Reference
<i>Coenobita</i>	<i>compressus</i>	Wenner, 1972
<i>Calcinus</i>	<i>laevimanus</i>	Wenner, 1972
	<i>latens</i>	Gherardi and McLaughlin, 1994
<i>Clibanarius</i>	<i>digueti</i>	Harvey, 1988
	<i>erythropus</i>	Gherardi, 1991
	<i>laevimanus</i>	Gherardi <i>et al.</i> , 1994
	<i>humilis</i>	Gherardi and McLaughlin, 1994
<i>Diogenes</i>	<i>brevirostris</i>	Walters and Griffiths, 1987
<i>Elassochirus</i>	<i>tenuimanus</i>	Abrams, 1988
<i>Paguristes</i>	<i>turgidus</i>	Abrams, 1988
<i>Pagurus</i>	<i>granosimanus</i>	Abrams, 1988
	<i>hirsutiuscudus</i>	Abrams, 1988
	<i>samuelsi</i>	Abrams, 1988
	<i>kennerlyi</i>	Abrams, 1988
	<i>beringanus</i>	Abrams, 1988
	<i>dali</i>	Abrams, 1988

inant in microhabitats without standing water at low tide; Abrams, 1988). The size of clustering species is also segregated within clumps (in *Clibanarius laevimanus*, Gherardi *et al.*, 1994). However, both sexes of *D. schmitti* are restricted within sabellarian bioherms (Gherardi and Cassidy, 1994b), starting from the late megalopa stage, and although the species has a contagious distribution (Gherardi and Cassidy, 1994b), clumps do not significantly differ in either sex ratio or size.

The sexual selection hypothesis

Under the rationale of the sexual selection hypothesis (Bertness, 1981a), the between-sex balance in the size distribution of *D. schmitti* implies that the two sexes get the same benefits (or handicaps) from larger dimension.

Reproductive potential might be enhanced with size. From the perspective of *D. schmitti* females, clutch size significantly increases with the body mass, and larger females also bear more voluminous eggs.

Larger size might also provide a higher reproductive potential to males. A sexual dimorphism was evident in the major chela dimensions (dactyl length, and palm length and width): the chela (especially the biggest) was more massive in the male than in the female. The functional significance of this sexual difference has been widely discussed for *Brachyura* (Hartnoll, 1974), where it was related to the use of chelipeds in territorial defense, combat, display, and courtship. In several hermit crabs, males showed complex precopulatory behaviors, involving the chelae, for example, either rotating and shaking the female (*Diogenidae*) or jerking her toward himself (*Paguridae*) (Hazlett, 1966, 1968). Sexual behavior has not yet been

observed in *D. schmitti*, but the importance for males of having larger chelipeds might be associated with the intrasexual competition to mate. Chelipeds are widely used in aggressive interactions, both in displays (cheliped extension, waving, and wig-wag display; F. Gherardi, in prep.), and in fights (hits and grasps), where the bigger and stronger the chelipeds are, the more likely the hermit is to win.

In hermit crabs, factors that could reduce the tendency to grow are the interspecific competition for shells and the scarcity of large housings within the habitat. By its ability to occupy empty polychaete tubes as a new housing, *D. schmitti* has freed itself from the harsh war for shells that occurs within the subtidal hermit crab assemblage in northern Puget Sound (Abrams *et al.*, 1986). Its small relative size must have preadapted this species to this narrow microhabitat, but its body mass is certainly constrained by the size distribution of the available empty tubes. In his ecological notes on the endemic Bermuda hermit *Calcinus verrilli*, Markham (1977) observed that the mean size of the crabs occupying attached vermetid shells was far smaller than that of crabs in mobile *Cerithium* shells. Members of the *D. schmitti* population analyzed here occupy the largest tubes at their disposal in the bioherm, and size in both sexes was positively correlated with tube opening, suggesting that crabs must change their housing with growth (Gherardi and Cassidy, 1994b).

The growth hypothesis

The growth hypothesis (Abrams, 1988) refers to the between-sex difference in the available energy for growth; the male-biased sex ratio in larger size classes in most hermit species is attributed to the additional energy that males can allocate to growth because they do not have to produce eggs (Bertness, 1981b). Data are still missing for the extent of growth through molts in *D. schmitti* and its energy-time budget is unknown, but a number of clues suggest that the distribution of the rhizocephalan parasites might affect growth in this species.

In the population we examined, the extent of infestation and parasite prevalence varied significantly between sexes, reaching in the males an average of 2.9 externae per individual and a percentage of 28 infested specimens. Prevalence is unaffected by the male host size, but the frequency of infested females decreases in the intermediate and larger size classes, where the infestation is significantly less diffused than in similar sized males.

Within the framework of the growth hypothesis, one likely conclusion drawn from these data is that if (1) the males are more frequently infected than the females, and if (2) parasites cause a reduction in the growth rate of the host, then the two sexes grow to the same extent because

the energy the females expend in producing eggs equals that which the males consume to support parasites. However, the two assumptions require further clarification and open new questions.

First, we do not know why the parasites are unequally distributed between the sexes. The observed pattern could not be explained by either an increased mortality rate of infested females or the occurrence of sex reversal, because the sex ratio was 50% in all the size classes. The attachment of the parasite larvae may be impeded by the efficiency of cleaning and grooming (Bauer, 1981), but the two sexes did not differ in either the extent or the modes of cleaning behavior (Gherardi, 1994). As a third explanation, immunological responses by the hosts might vary between sexes. Parasitized, but not normal, *Carcinus mediterraneus* have a substance in their blood that fixes complement in the presence of extracts of *Sacculina* (reviewed in Bang, 1983). However, in that parasitic relationship, electrophoregrams did not show any marked difference between the parasitized males and females (Herberts, 1978). *D. schmitti* females differ in their susceptibility to infection according to their reproductive states. No parasitized females have been found in ovigerous condition (other examples in Hoggarth, 1990, and Lützen and Jespersen, 1992; exceptions in Høeg and Lützen, 1985); one explanation is that parasitized females lose their eggs after a few days (Lützen and Jespersen, 1992), but the reasons remain unknown.

The second assumption, that growth rate of the host is affected by the parasite, is supported by the previous literature on rhizocephalan infestation (O'Brien and Van Wyk, 1984; Hawkes *et al.*, 1986; Hoggarth, 1990; Abelló and Macpherson, 1992; Bang, 1983; Overstreet, 1983). Nevertheless, a direct investigation of molt frequency is lacking and figures on the relative increase at ecdysis compared between infected and uninfected individuals are provided only by Lützen and Jespersen (1992). Our findings that parasites do not inhibit molting in *D. schmitti* or influence either body or cheliped weight in either sex make the growth hypothesis questionable, at least in this species.

Other effects of parasites

A variety of morphological and behavioral alterations exhibited by rhizocephalan-infected decapods and the hormonal involvement in those phenomena are extensively described by Hartnoll (1967), Nielsen (1970), and Phillips and Cannon (1978) among others (see, *e.g.*, bibliography by Overstreet, 1983). *D. schmitti* males do not undergo the process of feminization observed in other species (Hartnoll, 1982; O'Brien and Van Wyk, 1984), as evidenced by the preservation of some "maleness" characters (*e.g.*, the high relative depth of the major chela).

The only alteration is the frequent absence of the second pleopod, which cannot result from an attempt by the parasite to provide a safe accommodation for the externae, but seems instead to be a consequence of the eruption of *Peltogaster boschmae* externae within the soft tissue lining the host abdomen, which corresponds to the attachment point of the second pleopod.

Neither do infected hermits exhibit behavioral alterations, such as lethargy, that could decrease their ability in direct or exploitative competition: in the laboratory, parasitized and healthy *D. schmitti* had the same probability of getting an empty polychaete tube, and in the field, they occupied equally sized housings. Besides, relative weight, and thus possibly feeding efficiency, was unaffected by the presence of rhizocephalans. The only behavioral result of parasite manipulation is the initiation of mock parental care, in which infected hermits of both sexes ventilate *Peltogaster boschmae* externae in the same way that gravid females ventilate their eggs.

Reproductive patterns

D. schmitti females attain maturity at a relatively small size: the smallest egg-bearing specimen measured 1.1 mm SL. On the other hand, the allometry of chela growth should indicate that maturity (at least, functional maturity; Hartnoll, 1969) occurs in males at larger size (over 3.4 mm SL).

A precocious onset of sexual behavior in females has been reported in the decapod literature and associated with a reduced possibility of encountering males; in the parasitic females of the Pinnotheridae (Christensen and McDermott, 1958) and in the freshwater crab *Potamon fluviatile* (Micheli *et al.*, 1990) copulation can occur even in prepubertal females, and sperm are kept in the seminal receptacles until ovulation.

A second remarkable feature of reproduction is the low frequency (50%) of gravid females in all the size classes. This is particularly evident when we consider that *D. schmitti* breeds only once per year (Nyblade, 1974), and that the breeding period (January–April) is short, but the time necessary for eggs to mature is relatively long (exceeding, on average, 1 month).

One explanation is that due to the shortage of food, females may have limited energy for producing clutches, causing them to skip the reproductive season. If this were the case here, we should expect a gradient in the clutch size depending on the available energy. Nonetheless, egg number is a function of female size, and the latter is not related to feeding efficiency (Gherardi, 1994). In addition, the annual egg production (52.8 mg of eggs per 100 mg female weight per year; Nyblade 1974) is high compared with that of the other hermit crabs in northern Puget Sound.

Another hypothesis refers again to the difficulty that this sedentary species encounters in finding a mate. *D. schmitti* is gonochoristic and mating in hermit crabs requires copulation (Hazlett, 1966), but it is still unclear how this is effected in this species. Males, females, or both are assumed to leave the attached tube and roam about with their abdomens naked (or at best in broken pieces of tubes; Nyblade as reported by Caine, 1980) to seek receptive mates. Despite the clumped distribution of the population, this is a risky behavior; in the laboratory, wandering hermits inhabiting loose tubes are easy prey for the crabs and fishes (F. Gherardi, in prep.), that frequent sabellarian bioherms (Gherardi and Cassidy, 1994a).

Hatching lasts from 1 to 6 nights, the length of time being related to the overall number of larvae. This suggests either that development of embryos belonging to the same batch is out of phase or that hatching is controlled by the embryos themselves, by the females, or by both (Saigusa, 1992). Such an extension of hatching in sequential bursts might be a mechanism to allow survival of at least a number of larvae in a difficult, predator-filled, and unpredictable environment, such as the current-swept channels of Puget Sound.

In *D. schmitti*, hatching occurs exclusively at night, possibly to minimize predation on the newly released larvae by diurnal fishes. In contrast to the other decapods inhabiting enclosed habitats (estuaries and mangrove swamps; Forward, 1987; Hartnoll, 1988), in this species larval release is synchronized with neap tides, when the tidal current is consistently lower than in the spring phase. This timing seems to be controlled by an endogenous clock (De Vries and Forward, 1989), persisting under laboratory conditions in which the tidal cycle corresponding to the rhythm is absent. This pattern of larval release seems unrelated to salinity tolerance (Forward *et al.*, 1982), because salinity is nearly constant in the examined area (SPMC, 1992). Its adaptive meaning is suggested by *D. schmitti*'s behavioral ecology. For this species—so dependent upon a habitat (sabellarian bioherms) that is rare and quite unpredictable (Gherardi and Cassidy, 1994a)—it is more beneficial if larvae are retained within the basin near the parental population than if they are flushed out to open waters for planktonic development (see McConaughy, 1992, for a discussion of larval retention *vs.* dispersal in decapods).

Acknowledgments

We thank Dr. Jorgen Lützen (University of Copenhagen) who kindly identified parasites of *D. schmitti*. The study was encouraged by Dr. Patsy A. McLaughlin (Shannon Point Marine Center, WWU), to whom we are greatly indebted. Part of the work was conducted at the

Shannon Point Marine Center, Anacortes, Washington. Partial funding was provided by M.U.R.S.T. to the first author.

Literature Cited

- Abelló, P., and E. Macpherson. 1992. Epibiosis and rhizocephalan infestation patterns in relation to the reproductive biology of *Lithodes ferax* (Filhol, 1885) (Anomura: Lithodidae). *J. Crustacean Biol.* **12**: 561–570.
- Abrams, P. A. 1988. Sexual difference in resource use in hermit crabs; consequences and causes. Pp. 283–296 in *Behavioural adaptation to the Intertidal Life*. G. Chelazzi and M. Vannini, eds. Plenum Press, New York.
- Abrams, P., C. Nyblade, and S. Sheldon. 1986. Resource partitioning and competition for shells in a subtidal hermit crab species assemblage. *Oecologia* **69**: 429–445.
- Bang, F. B. 1983. Crustacean disease responses. Pp. 113–153 in *The Biology of Crustacea*. Vol. 6, *Pathobiology*, A. J. Provenzano, Jr., ed. Academic Press, New York.
- Bauer, R. F. 1981. Grooming behavior and morphology in the decapod Crustacea. *J. Crustacean Biol.* **1**: 153–173.
- Bertness, M. D. 1981a. Interference, exploitation, and sexual components of competition in a tropical hermit crab assemblage. *J. Exp. Mar. Biol. Ecol.* **49**: 189–202.
- Bertness, M. D. 1981b. Competitive dynamics of a tropical hermit crab assemblage. *Ecology* **62**: 751–761.
- Caine, E. A. 1980. Adaptations of a species of hermit crab (Decapoda, Paguridea) inhabiting sessile worm tubes. *Crustaceana* **38**: 306–310.
- Christensen, A. M., and J. J. McDermott. 1958. Life-history and biology of the oyster crab, *Pinnotheres ostreum* Say. *Biol. Bull.* **114**: 146–179.
- De Vries, M. C., and R. B. Forward, Jr. 1989. Rhythms in larval release of the sublittoral crab *Neopanope sayi* and the supralittoral crab *Scarmma cinereum* (Decapoda: Brachyura). *Mar. Biol.* **100**: 241–248.
- Forward, R. B., Jr. 1987. Larval release rhythms of decapod crustaceans: an overview. *Bull. Mar. Sci.* **41**: 165–176.
- Forward, R. B., Jr., K. Lohmann, and T. W. Cronin. 1982. Rhythms in larval release by an estuarine crab (*Rhithropanopeus harrisi*). *Biol. Bull.* **163**: 287–300.
- Gherardi, F. 1991. Relative growth, population structure, and shell-utilization of the hermit crab *Clibanarius erythropus* in the Mediterranean. *Ochalia* **17**: 181–196.
- Gherardi, F. 1994. Multiple feeding techniques in the sessile hermit crab *Discorsopagurus schmitti*, inhabiting polychaete tubes. *Oecologia* **98**: 139–146.
- Gherardi, F., and P. M. Cassidy. 1994a. Macrobenthic associates to the polychaete *Sabellaria cementarium* bioherm from northern Puget Sound, Washington. *Can. J. Zool.* **72**: 516–525.
- Gherardi, F., and P. M. Cassidy. 1994b. Sabellarian tubes as the housing of *Discorsopagurus schmitti*. *Canad. J. Zool.* **72**: 526–532.
- Gherardi, F., and P. A. McLaughlin. 1994. Shallow-water hermit crabs from Mauritius and Rodrigues Islands, with the description of a new species of *Calcinus*. *Raffles Bull. Zool.* **42**: 613–636.
- Gherardi, F., F. Zatterli, and M. Vannini. 1994. Hermit crabs in a mangrove swamp: the structure of *Clibanarius laevimanus* clusters. *Mar. Biol.* **121**: 41–52.
- Hartnoll, R. G. 1967. The effects of sacculinid parasites on two Jamaican crabs. *J. Linn. Soc. London Zool.* **46**: 275–295.
- Hartnoll, R. G. 1969. Mating in the Brachyura. *Crustaceana* **16**: 11–181.
- Hartnoll, R. G. 1974. Variation in growth pattern between some secondary sexual characters in crabs (Decapoda Brachyura). *Crustaceana* **27**: 131–136.

- Hartnoll, R. G. 1982. Growth. Pp. 111–196 in *The Biology of Crustacea*. Vol. 2, *Embryology, Morphology and Genetics*, L. G. Abele, ed. Academic Press, New York.
- Hartnoll, R. G. 1988. Eco-ethology of mangroves. Pp. 477–489 in *Behavioural Adaptation to the Intertidal Life*, G. Chelazzi and M. Vannini, eds. Plenum Press, New York.
- Harvey, A. W. 1988. Size- and sex-related aspects of ecology of the hermit crab *Clibanarius digneti* Bouvier (Decapoda: Anomura: Diogenidae). Ph.D. dissertation. University of Arizona, Tucson, AZ.
- Hawkes, C. R., T. R. Meyers, T. C. Shirley, and T. M. Koehnman. 1986. Prevalence of the parasitic barnacle *Briarosaccus callosus* on king crabs of southeastern Alaska. *Trans. Am. Fish. Soc.* **115**: 252–257.
- Hazlett, B. A. 1966. Social behaviour of the Paguridae and Diogenidae of Curaçao. *Stud. Fauna Curaçao Other Caribb. Isl.* **23**: 1–143.
- Hazlett, B. A. 1968. The sexual behavior of some European hermit crabs (Anomura: Paguridae). *Pubbl. Stn. Zool. Napoli* **36**: 238–252.
- Herberts, C. 1978. Relation hôte-parasite entre *Carcinus mediterraneus* and *Sacculina carcini*; analyse immunochimique et mise en évidence d'une précipitine antisacculine. *C. R. Acad. Sci.* **286**: 725–728.
- Hoeg, J. T., and J. Lützen. 1985. Crustacea Rhizocephala. Pp. 1–92 in *Marine Invertebrates of Scandinavia*, Vol. 6. Norwegian University Press, Oslo.
- Hoggarth, D. D. 1990. The effects of parasitism by the rhizocephalan, *Briarosaccus callosus* Boschma on the lithodid crab, *Paralomis granulosa* (Jacquinot) in the Falkland Islands. *Crustaceana* **59**: 156–170.
- Lützen, J. 1992. Morphology of *Thompsonia reinhardi*, new species (Cirripedia: Rhizocephala), parasitic on the northeast Pacific hermit crab *Discorsopagurus schmitti* (Stevens). *J. Crustacean Biol.* **12**: 83–93.
- Lützen, J., and A. Jespersen. 1992. A study of the morphology and biology of *Thompsonia littoralis* (Crustacea: Cirripedia: Rhizocephala). *Acta Zool.* **73**: 1–23.
- Margolis, L., G. W. Esch, J. C. Homes, A. M. Kuris, and G. A. Schad. 1982. The use of ecological terms in parasitology. *J. Parasitol.* **68**: 131–133.
- Markham, J. C. 1977. Preliminary note on the ecology of *Calcinus verrilli*, an endemic Bermuda hermit crab occupying attached vermetid shells. *J. Zool. (Lond.)* **181**: 131–136.
- McConaughy, J. R. 1992. Decapod larvae: dispersal, mortality, and ecology. A working hypothesis. *Am. Zool.* **32**: 512–523.
- McLaughlin, P. A. 1974. The hermit crabs (Crustacea Decapoda, Paguridea) of Northwestern North America. *Zool. Verhand.* **130**: 1–396.
- Micheli, F., F. Gherardi, and M. Vannini. 1990. Growth and reproduction in the freshwater crab, *Potamon fluviatile* (Decapoda, Brachyura). *Freshwater Biol.* **23**: 491–503.
- Nielsen, S. O. 1970. The effects of the rhizocephalan parasites *Pelto-gaster paguri* Rathke and *Gemmosaccus sulcatus* (Lilljeborg) on five species of paguridan hosts (Crustacea Decapoda). *Sarsia* **42**: 17–32.
- Nyhlade, C. F. 1974. *Coexistence in Sympatric Hermit Crabs*. Ph.D. dissertation. University of Washington, Seattle, WA.
- O'Brien, J., and P. Van Wyk. 1984. Effect of crustacean parasitic castrators (Epicaridean isopods and Rhizocephalan barnacles) on growth of crustacean hosts. *Crustacean Issues* **3**: 191–218.
- Overstreet, R. M. 1983. Metazoan symbionts of crustaceans. Pp. 155–250 in *The Biology of Crustacea*, Vol. 6, *Pathobiology*, A. J. Provenzano, Jr., ed. Academic Press, New York.
- Phillips, W. J., and L. R. G. Cannon. 1978. Ecological observations on the commercial sand crab, *Portunus pelagicus* (L.), and its parasite, *Sacculina granifera* Boschma, 1973 (Cirripedia: Rhizocephala). *J. Fish. Dis.* **1**: 137–149.
- Saigusa, M. 1992. Control of hatching in an estuarine terrestrial crab. I. Hatching of embryos detached from the female and emergence of mature larvae. *Biol. Bull.* **183**: 401–408.
- Siegel, S. 1956. *Nonparametric Statistics for the Behavioral Sciences*. McGraw-Hill, New York.
- SPMC. 1992. *Water Quality Record* Annual Report from Shannon Point Marine Center, Anacortes, WA.
- Walters, W. L., and C. L. Griffiths. 1987. Patterns of distribution, abundance and shell utilization amongst hermit crabs, *Diogenes brevis*. *S. Afr. J. Zool.* **22**: 269–277.
- Wenner, A. M. 1972. Sex ratio as a function of size in marine Crustacea. *Am. Natur.* **106**: 321–350.
- Zar, J. H. 1984. *Biostatistical Analysis*. Prentice-Hall, Englewood Cliffs, NJ.